Demographic variation in two forest populations of oribatid mites

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Horacio Vera

Seccion Ecologia, Facultad de Ciencias, Universidad de la Republica, Calle Tristan Narvaja 1674, 11200 Montevideo, Uruguay

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Summary. Two populations of *Platynothrus peltifer* living in an oak forest and in a larch plantation were studied. Number density is higher in the oak site while mites from this very site present the highest fecundity when feeding is oak leaves. Mites from the larch site had similar fecundities regardless of the food they have. The survival of mites from each site and with a distinctive food does not present any difference. Increased temperature, by contrast, decreased survival. Mites from the oak site fed with oak leaves had higher pellet production than did mites from the same site fed with larch needles. On the contrary, mites from the larch site present equal metabolism values whichever food they have. Finally, these observations suggest that the nutritional resources of mites from the larch plantation are more diversified than are those of mites from the oak site. The trophic niche breadth of the former is larger than the one of the latter, but in contrast, the niche of the population from the oak site is more specialised.

Key words: density, fecundity, survival, moulting, niche, Acari, Platynothrus peltifer

Introduction

The presence of the same Oribatid species on very different soils is a very well known fact (e.g. Anderson, 1975; Seastedt, 1984; Usher, 1985; Webb, 1989). One of these species is Platynothrus peltifer Koch, 1839 (Lebrun, 1971; Wauthy, 1982) whose biology is very well known (Taberly, 1958 a & b; Block, 1965; Harding, 1973). Recently, Vera and Berthet (1988) reported important differences on moulting frequency and survival rate (measured in laboratory conditions) on immature individuals of two populations of Platynothrus peltifer coming from an oak forest (Quercus petrae) and a larch plantation (Larix europea). Moreover, an elecrophoretical study of three enzymes (superoxidedismutase, esterase and malate-dehydrogenase) measured the genetic identity between both populations. The study result is comparable to values commonly reported for conspecific, geographical populations (Vera et al., 1990).

The population differences found showed a good separation between the two populations whose individuals presented distinctive reactions when they were in so different environments. Therefore, it seems that spatio-temporal dynamics of each population [e.g. number (a population) density, fecundity, mortality and age distribution] might be different. The study of other population parameters was carried out in order to check this hypothesis. In order to do that, a systematic sampling of both populations and several experiments were conducted. Therefore, the description of the natural cycle of both populations and consequently the parameters which differentiate them were established. Furthermore, the interactions of these organisms with the edaphic mycoflora, which has an important influence over the dynamics of the two Oribatid populations, were researched. P. peltifer

is a detritivorous and fungal-feeder species (Luxton, 1972; Petersen & Luxton, 1982), and this characteristic partially explains its aggregated spatial distribution. On the other hand, Mitchell & Parkinson (1976) reported that the development of fungus in certain parts of the plant as it decays has an important effect on mite population dynamics just like on the community structure either as a source of feeding or by toxin production. The laboratory experiments were limited to certain aspects of the species' trophic niche, in other words, its response to the feeding changes in order to establish the influence of feeding on certain demographic parameters.

Material and methods

Sites

Both sites are situated in Belgium (50° 41' N and 4° 36' E). The study was carried on from May 1982 to May 1985.

The first site is placed in an oak forest. Humus is a modermull type with a pH 5 The organic horizons O_1 , O_h and O_f are each 1 cm deep and the Ah_1 horizon is 3 cm deep. The second site is placed in a larch plantation with humus of moder type. The organic horizons O_1 , O_f and O_h are 1.0-1.5 cm, 2-3 cm and 1 cm deep respectively while the Ah_1 horizon is 1 cm deep. The criterion for establishing the spatial limits of the stations was the homogeneous distribution of, at least, one bushy plant species. This was established following Braun-Blanquet's system of rating, where two scales are used, one combining the number and cover of a species, and the second giving a measure of the grouping (Kershaw, 1975) In the oak forest, the species with homogeneous distribution was *Prunus serotina* (Ehrh.) [Braun-Blanquet's rating: 5.4] while in the larch plantation it was *Pteridium aquilinum* (5.5). Further information about both stations is given elsewhere (Vera & Berthet, 1988).

Sampling

Weekly samplings were accomplished during three years. Twelve samples were taken every week. Each sample was taken using a cylindrical core of $16\,\mathrm{cm^2}$. The division of the station in quadrats of $1\,\mathrm{m^2}$ provided a random sampling of the population. All the organic horizons of the soil (O₁, O_f and O_b) as well as the Ah₁ horizon were taken in each sample. The depth of each core depended on the depth of the horizons (see 2.1. Sites). The edaphic fauna was extracted with Berlese funnels, for three weeks, in 75% ethanol.

The larvae and adults of this species are easy to separate since the larvae have six legs and the adults are much darker than the other stases (sensu Granjean, 1938). The three nymphal stases were separated by size. From a random sampling of 200 individuals of each stase it was determined that protonymphs measure between 330 and 462 μ m, deutonymphs between 486 and 618 μ m, and tritonymphs between 636 and 792 μ m.

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Laboratory experiments

- I A former set of observations was made on young adults in order to determine the Ro (Begon et al., 1986, page 153) of the cohorts, as well as their mean fecundities, which were compared by a Wilcoxon's test (Dagnelic, 1975). The value of their mean life (calculated as the number of days during which a cohort reduces in a half) was also determined. The young adults are easily distinguished by their light brown color and were obtained using Berlese funnels. They get darker at the age of 10-15 days. A group of 180 young adults was divided in six groups of 30 young adults each and placed in rearing cups (of 3.6 cm of diameter and 2.5 cm high). Each cup was weekly looked over, counting and picking out eggs and dead individuals. In the experimental plan three variables were taken into account:
- (1) The original environment they came from.
- (2) The type of food given: all of them ate the fungus *Ulocladium consontiale* (Thümen et Simmons). Besides, one of them had *Quercus* leaves and the others *Larix* leaves.
- (3) The temperatures at the cups were: 25 °C, 14 °C, and the laboratory temperature, between 19 °C to 20 °C.
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II - A second set of observations was made on adults picked up in each year season. This was done in order to determine the importance of three variables: (1) original environment, (2) type of given food, and (3) season of the year on the pellet production of mites. The adults were put in 16 rearing cups, 8 of each containing 30 adults coming from the oak forest and the other 8 with 30 adults coming from the larch plantation. Temperature for both groups was 19-20 °C. Half the adults from the two sites were fed with Quercus leaves, and the other half with Larix leaves.

Observations on the adults were done every 24 hours during a week, when pellets were counted and picked out. A three way analysis of variance using numbers of pellets in every cup was accomplished. Pellet production was assumed as being a partial way of measuring the digestive metabolism of mites.

III - An analysis to determine the C/N of the organic horizons was carried out with the random samples of both sites.

Results

Sampling

Larvae: Larvae hatch at the same time in both populations in natural environment. They appear in the middle of summer to disappear in early winter, with a peak in abundance at the beginning of autumn. The number of larvae at the oak station was practically the same (685, 667 and 651) during the three years of sampling (fig. 1 A). Otherwise, in the larch plantation, this number changed very much from one year to the other (1592, 582 and 401) (fig. 2A).

Protonymphs: This stase is present approximately at the same period of the year in both stations. The time of hatching is variable in Larix plantation (fig. 2A), but not in oak site where hatching occurs always in August (fig. 1A). At Quercus station, the number of protonymphs increases progressively having a maximum in December and decreases slowly afterwards. By contrast, the Larix population does present a peak of abundance.

Deutonymphs: This stase hatches after the period of abundance of protonymphs, having a peak of abundance in April. Comparing the two site populations, the deutonymphs are present for only 8 months in the oak forest (fig. 1B) while in larch plantation this stase is present the whole year (fig. 2B).

Tritonymphs: Tritonymphs are present in the Larix plantation (fig. 2B) during the whole year while they are completely absent in the oak site for several months (from September

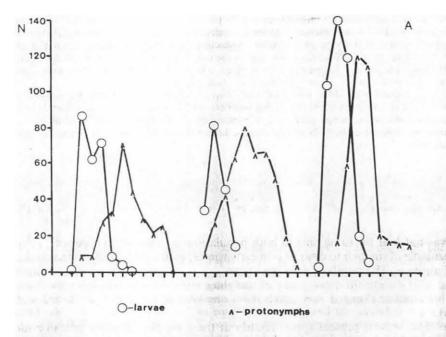
Adults: This stase is present during the whole year in both stations without a peak of abundance. Young adults are present during September and October before larvae appear. Number density: Both sites present the same mite number density, counted as number of individuals per organic horizon surface (8000 mites/m² for larch plantation and 7600 mites/m² for oak site). These figures have an evident bias since the thickness of the organic horizons is bigger in the larch plantation than in the oak forest.

In order to quantify the relative importance of each horizon the dry weights of the samples were compared. The average dry weight of a core of oak site is 7.77 g ($s^2 = 5.62$) and 11.72 g ($s^2 = 6.00$) in larch site. If number density is stated in number of mites/100 g of dry organic matter, 97812 mites/100 g in the oak site against 68269 mites/100 g in the larch plantation is obtained.

Laboratory experiments

I - Adults from the oak site fed with larch leaves had much lower fecundities than did those fed with oak leaves. These fecundities show significant differences when Wilcoxon test is applied (fig. 3).

The adults of the larch site had similar fecundities regardless of food, testing in all cases non significant differences (fig. 3).



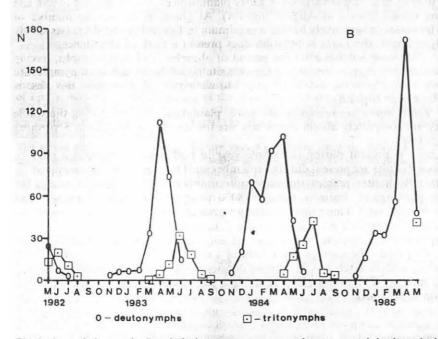
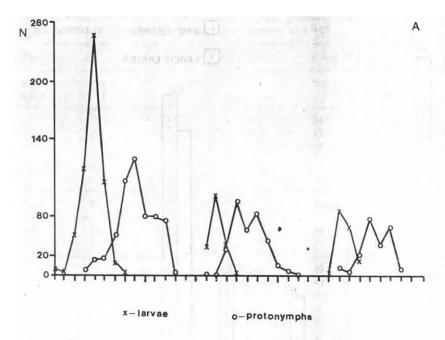


Fig. 1. Annual changes in P. peltifer immatures mean number per month in the oak site. A — Larvae and protonymphs. B — Deutonymphs and tritonymphs.

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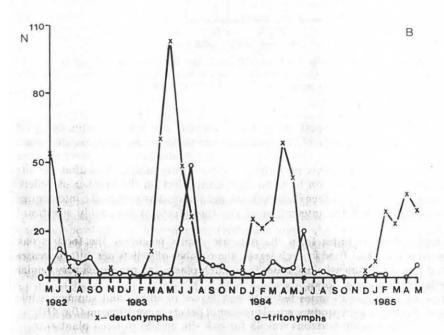


Fig. 2. Annual changes in P. peltifer immatures mean number per month in the larch site. A — Larvae and protonymphs. B — Deutonymphs and tritonymphs.

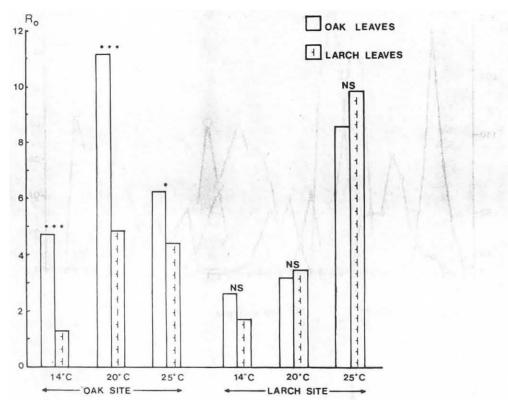


Fig. 3. Values of Ro for P. peltifer adults from oak and larch sites fed with oak or larch leaves, and reared at three temperatures. (Above the histogrammes results of Wilcoxon test where averge fecundity of these adults is compared. NS = non significant, *P < .05, ***P < .001).

The survival of adults with an equal original environment and with a distinctive food does not present any difference (table 1). Increased temperature, by contrast, decreased survival.

II — The results of the experiments performed for pellet production show that the site as well as the interaction site-season have no significant effect on the number of pellets. On the other hand, the effect of other factors (food and seasons) as well as the interactions (site-food, food-seasons and the interaction of the three factors) are highly significant (table 2, fig. 4).

The highest metabolism of mites from the oak site occurs whenever the food is oak leaves, on the contrary, when food is larch leaves, the number of pellets per mite decreases to less than half (fig. 4A). Nevertheless, mites from larch plantation produce a very similar number of pellets regardless of food.

This number is much higher in mites fed with oak leaves in spring and summer, while those mites fed with larch leaves produce equal number of pellets in every season (fig. 4B). III — The C/N of the organic horizons was 48 for oak site and 55 in larch plantation.

Discussion

Differences in temporal dynamics of both populations suggest that, in the larch plantation, deutonymphs and tritonymphs' moulting frequency is very small, mostly on tritonymphs'

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Table 1. Values of "mean life" (D) provided for adult populations of Platynothrus peltifer, calculated as the number of days during which a cohort reduces in a half

Site	D		Site	Food		
oak larch	354 354	- W.		oak	D	larch
			oak larch	343 377		343 322
		200				
Food	D		Food	Tempera	ture (°C)	
oak larch	360 333			14	20 D	25
			oak larch	591 497	313 312	222 210
Tempera- ture (°C)	D		Tempera- ture (°C)	Site		
14 20 25	538 318 225			oak	D	larch
	223	The sa	14 20 25	516 327 212		560 310 237

Note: Twelve cohorts were established: mites sampled in oak and larch sites, fed with oak or larch leaves and reared at 3 temperatures (14, 20 and 25 °C)

stase. This is probably an environmental factor (just like feeding), which stops a tritonymphs' quick moulting. Therefore, it does not seem possible to explain this later moulting due to certain type of genetic determinism. That is the longer the tritonymphs live the better fitness to the larch environment they have. However it seems to be exactly the opposite case since the species presents a short reproduction period (activity performed by young adults), beginning in early summer. Therefore, only the presence of young adults assure reproduction at the single moment it takes place. The lower moulting frequency of deutonymphs and tritonymphs from the larch site (Vera & Berthet, 1988) explains its constant presence in this environment. On the other hand, these two stases show an equal survival rate at both sites (Vera & Berthet, 1988).

The difference of density presented by both populations is conspicuous. There is evidence that the oak site is the most suitable environment for the species of the two sites considered in this paper.

Dynamics also differ at the larval level. Larval number is constant every year at the oak site and unstable at larch site. Nevertheless, reasons for these remain obscure since no modification of the site was recorded during the studied period.

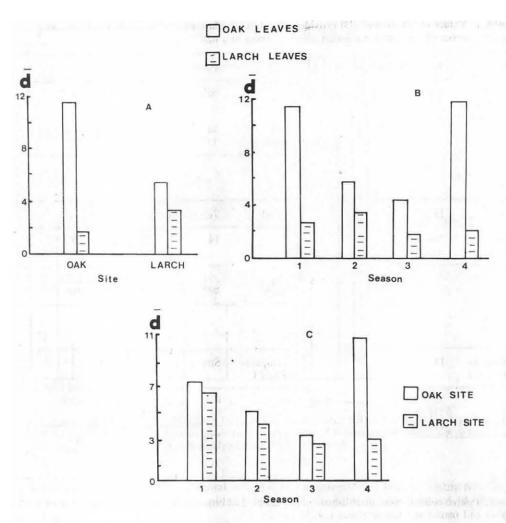


Fig. 4. Effects of two-factor interactions on the average number of pellets per individual (d) per day produced by *P. peltifer* adults.

A - Adults from the oak site fed with oak leaves or larch leaves, and adults from the larch site fed with oak leaves or larch leaves.

B - Adults from both sites fed with oak leaves or larch leaves, for each of four seasons (1-summer, 2-autumn, 3-winter, 4-spring).

C - Adults from the oak site fed with oak leaves or larch leaves, and adults from the larch site fed with oak leaves or larch leaves, for each of four seasons.

In spite of the differences already mentioned, life cycle of both populations presents some similarities. In fact, periods of abundance of immature stases occur at the same time in both sites.

The results about the adult fecundity show that mites from larch plantation are able to exploit two different food resources while mites from the oak site are able to exploit only one. In fact, fecundity of the mites belonging to the larch site is not modified with feeding but they present the same fecundity regardless of their food. By the contrary, mites from the oak site have a high fecundity only when they are able to feed with leaves from their original site. Their trophic niche is, therefore, more restricted and their fecundity is decreased when changing the type of feeding.

Table 2. Total number of pellets, per week, and per rearing cup (I, II, III and IV, 30 mites per cup) produced by *P. peltifer* adults

Site	Food	Season	I	II		III	IV	Total
	175	1	249	588	15	469	241	1547
	oak	2	233	120		98	397	848
	4.0 7921	3	116	131	and the	176	210	633
oak	1	4	585	584		695	572	2436
					4 P			
		1	50	34		70	35	189
	larch	2	81	63		92	103	339
		3	29	42		19	44	134
		4	34	27		32	32	125
	(1	353	193		365	231	1142
	oak	2	61	124	1	220	141	546
		3	109	83	and.	87	87	366
larch	{	4	95	110		79	90	374
		1	93	123		96	92	404
	larch	2	121	111		143	91	466
		3	65	73		76	61	275
		4	81	79		99	98	357

Seasons: 1-summer, 2-autumn, 3-winter, 4-spring.

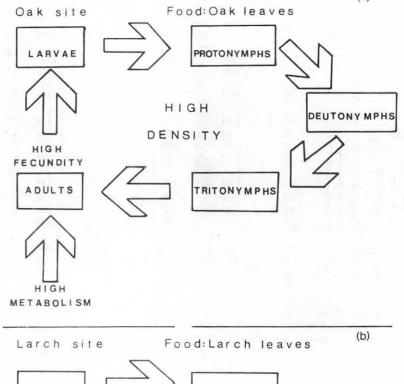
S-NS. F ***. SE ***. S × F ***. F × SE ***. S × SE *. S × F × SE ***. S, N, and SE with asterisks denote the significance levels of the effects of Site, Food and Seasons, and S × F, F × SE, S × SE, and S × F × SE with asterisks denote the effects of Site × Food, Food × Seasons, Site × Seasons, and Site × Food × Seasons interactions on the pellet production of P. peltifer adults as determined by 3-way ANOVA (log₁₀ transformation). *P < .05, ***P < .001, NS = non significant

On the other hand, survival is equal for *P. peltifer* whichever the original site or feeding is. Though feeding has a considerable effect on fecundity, survival is not affected by this factor. This means that adults of the species are able to live in very different habitats even though feeding resources are not the best. In this suboptimum condition, population does not increase due to their low fecundity. These demographic characteristics seem to be an explanation for two observed phenomena (a) lower number density of the larch population if compared with the oak site, and (b) wide distribution of the species and its presence in so different biotopes.

The exclusive adaptation of the mites from the oak site to the feeding of their original environment is clear since their metabolism abruptly decreases when feeding is changed. On the contrary, metabolism from the mites belonging to the larch site is very similar whichever the feeding is. It appears that the population of the larch plantation is capable of using the most variable resources, and the population from the oak site uses much more specific feeding resources.

Those mites fed with oak leaves present a high increment on metabolic activity in spring and summer. This increment might be explained by the increase of their energetic needs related with their reproductive activity, which starts in this period. Therefore, the leaf decomposition rate might have also a role in the metabolic increment [the abundance of microorganisms as the plant decays is higher in these seasons (Bocock et al., 1960; Martinez et al., 1980). It has already pointed out that P. peltifer feeds preferentially on leaves where decomposition has already taken place.

This metabolic peak is not observed among mites fed with larch leaves; Debry (1980) reported that the increase of fungal populations on these leaves is much less than those on the oak leaves.



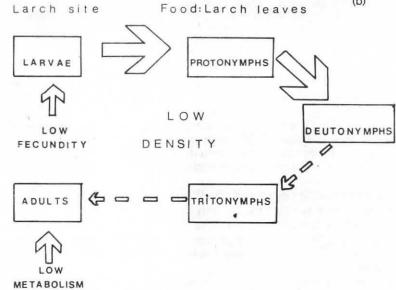


Fig. 5. The temporal dynamics of *P. peltifer* in both sites, related to the results of laboratory experiments and sampling. (See text for further explanation).

Otherwise, the oak C/N is inferior (35-45) to the larch C/N (> 60) (Duchaufour, 1977). The C/N in larch plantation is rather inferior to the average already mentioned above. It must be considered that ferns are very abundant in this site and that bushy species play an important role in the C/N (Duchaufour, 1965). Food given to these mites was exclusively larch leaves.

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In fig. 5a summary of the temporal dynamics of *P. peltifer* in both sites, in relation to the obtained laboratory experiment results, is shown. The size of the arrows is proportional to the value of the measured parameter (immatures' moulting frequency and survival rate, and adults' metabolism and fecundity). (A) Moulting and survival rates on immatures are high as adults' fecundity; the annual cycle of the species is completed with no difficulty. This "ideal" conditions determine a high number density. (B) Moulting frequency of larvae and protonymphs is high, on the contrary deutonymphs and tritonymphs moulting frequency is slow but their survival is high (Vera & Berthet, 1988) being then present constantly in this site. Adult fecundity is much lower in this site than in the oak site. All these factors determine a low population density.

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